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COMPARISONS OF SEXUAL AND APOGAMOUS RACES IN THE FERN GENUS PELLAEA

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Apogamy in ferns is of the obligate type involving changes in the gametophyte eliminating fertilization by absence or non-function of the archegonia. This is correlated with a compensating system in the sporophyte, circumventing the reduction in chromosome number by changes in the mitotic or meiotic divisions in the sporangium, prior to spore formation. Thus both gametophyte and sporophyte stages have the same chromosome number. This synchronized apogamous system is particularly remarkable for it evidently has been independently initiated more than once in 25 of some 209 genera of the Filicopsida which are cytologically known.

This study in *Pellaea*, on some morphological modifications which are associated with apogamy, was made with the purpose of understanding the evolutionary role of the mechanism in this group, against a background of rapidly increasing information on the frequency of the phenomenon in the Pteridophyta.

Apogamous ferns are considered to be of hybrid origin by Manton (1950, 1961) and Walker (1966) and there is support for this view in the following survey of chromosome levels and the apogamous condition. Data are drawn from the reports of chromosome numbers in the Filicopsida by Chiarugi (1960) and Fabbri (1963, 1965). An analysis of these records shows apogamy in 32 diploids in 9 genera, 66 triploids in 15 genera, 15 tetraploids in 6 genera, 5 pentaploids in four genera and one hexaploid and one octoploid. About 73% of these apogamous forms are at polyploid levels while 27% are apparent diploids, although the latter may not represent base numbers of the genera. The large proportion of apogamous forms at polyploid levels supports the hypothesis of a relationship of apogamy with hybridization. However, the percentage of diploids is a significant one and the origin of apogamy in these is not apparent.

In some genera, as *Pteris*, apogamy is especially frequent, and it is reported by Walker (1962) in 16 diploids, 14 triploid and 9 tetraploid forms. In *P. cretica* apogamy occurs in diploid, triploid and tetraploid forms and it also occurs in *P. biaurita* at diploid and triploid levels and in triploids and tetraploids in *P. quadriaurita*. In *Adiantum*, apogamy is reported in five diploid, three triploid and one hexaploid member. In *Dryopteris* five diploids and 16 triploids are apogamous, and in *D. Borreri* it is known at diploid, triploid, tetraploid, and pentaploid levels. In contrast to these, there are some large genera such as *Asplenium*, in which apogamy is infrequent with reports of only three triploid, one pentaploid, and two octoploid members, and it is not, or doubtfully, reported in *Blechnum*, *Cyathea* and *Thelypteris*. Thus, while apogamy is prevalent in some groups and absent in others it is notable that it occurs in a number of genera which are only distantly related.

Some information on the origin of apogamy in ferns comes from experimental studies on induced apogamy in gametophytes in which there appears to be a genetic predisposition for the condition. In these, apogamy is influenced by environmental changes such as drying, light intensity and in increased concentration of certain sugars. In some of these studies, as those by Whittier (1964), it is recognized that the induction of apogamy is more readily accomplished in certain "races" of a species than in others. The genetic control of apogamy as a dominant is demonstrated by experiments on *Pteris* by Walker (1962) where crosses made between apogamous diploids and sexual species produce only apogamous forms. Dominance may be effective in perpetuating and increasing the number of apogamous forms by crosses involving antherozoids from apogamous plants. This may account for the frequency of apogamy in certain groups as *Pteris*, *Adiantum* and *Pellaea*.

There have been several studies of apogamy in *Pellaea* and it is known in six of the 15 species in section *Pellaea*. The triploid species *P. atropurpurea*, reported by Manton (1950) and a triploid variety in *P. sagittata*, noted by Tryon & Britton (1958) appear to be of hybrid origin. Apogamy is reported here in three species of section *Pellaea* belonging to the "light-stiped" group which represent a separate evolutionary line in the section. This record of apogamy in a distinct species-group is in harmony with reports of its occurrence in different genera and is indicative of independent origins of the mechanism. These three closely related species — *P. andromedifolia* (Kaulf.) Fée, *P. intermedia* Mett. ex Kuhn and *P. ovata* (Desv.) Weatherby — are exceptional in the ferns for each has both sexual diploid and apogamous triploid races. The triploid chromosome level of the apogamous types shows a relationship to hybridization. The morphological similarity of the sexual and apogamous races in each of the species is suggestive of a close relationship between the putative parents. Comparative studies were made of the chromosome numbers, gametophytes, juvenile leaves, guard cell size and spore size for the two forms in each species. Comparisons are also drawn with a sexual diploid and sexual tetraploid in *P. ternifolia* (Cav.) Link var. *ternifolia* (later referred to by the species name only), also a member of Section *Pellaea* but belonging to a "dark-stiped" group, as a basis for comparison of polyploidy without apogamy. Geographic distributions of the races are compared as a measure of the evolutionary success of the different forms. Most of the apogamous members in Section *Pellaea* are widely distributed in North America or also South America while most sexual members have more limited ranges.

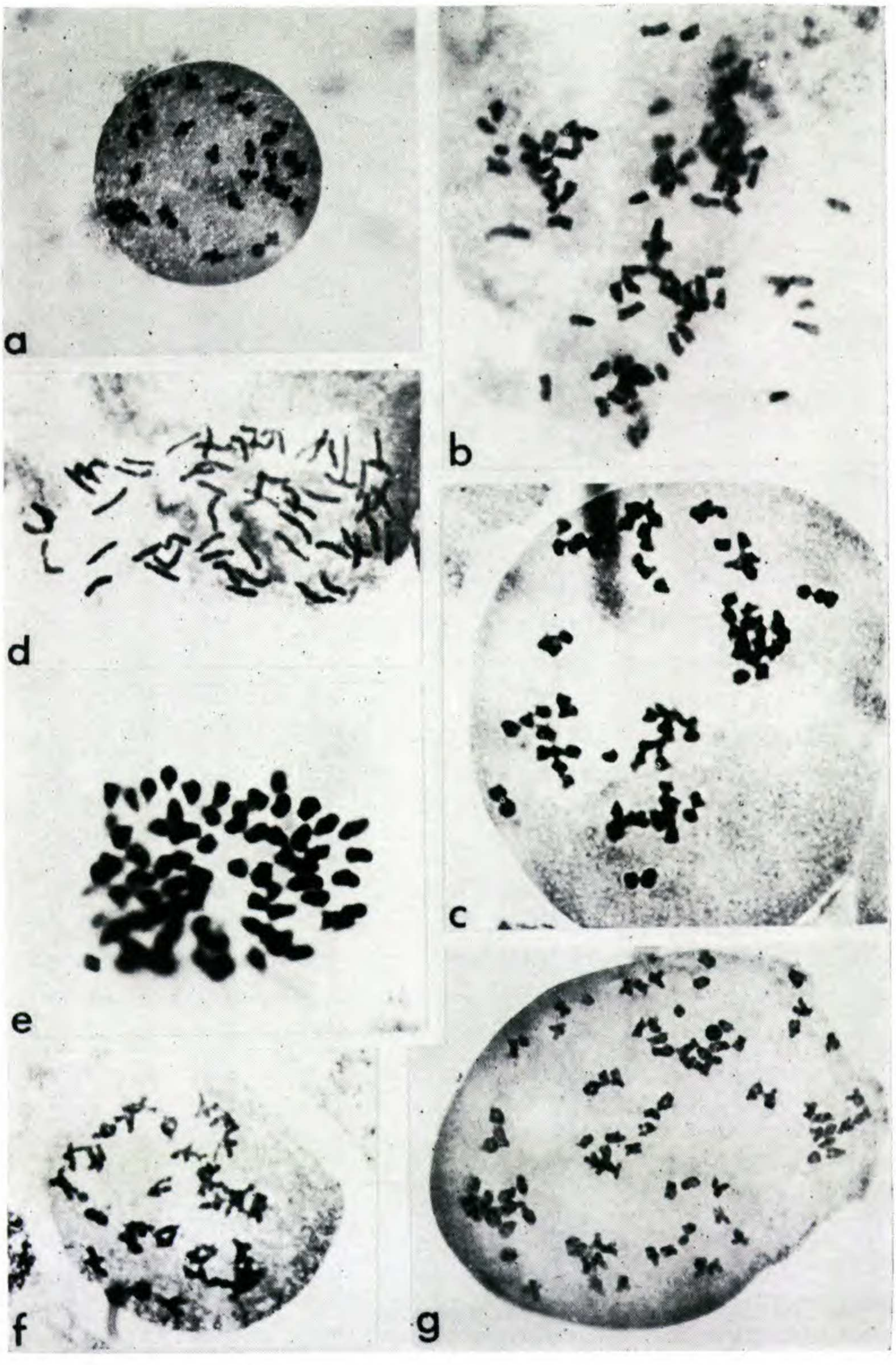

Fig. 1. a-c. *Pellaea andromedifolia,* squash preparation of meiosis. a. Sexual diploid, n = 29, San Gabriel Mts. Calif., × 650. b. Apogamous triploid, "n" = 87, Humboldt Co., Calif., × 1650. c. Apogamous

Material and Methods

Measurements and cytological reports in this study were obtained from original collections, or plants grown from spores obtained from them, maintained in a greenhouse for a period of two to six years. Field studies and collections were made with R. M. Tryon in the western United States and Mexico in 1950, 1956 and 1957. Collections from the first trip are deposited at the Missouri Botanical Garden. Some duplicates of these, those from the last two trips, as well as cytological vouchers, are deposited at the Gray Herbarium. Meiotic chromosome counts reported here were obtained by the standard fixation in 3:1 alcohol and acetic acid and stained in acetocarmine as described by Manton (1950). The same fixative and stain were used for the mitotic cells from root tips and this material was treated with snail cytase following the procedure reported by Fabergé (1945). The snail enzyme breaks down the middle lamella and allows the chromosomes to spread freely when pressure is applied.

Distribution records were plotted from specimens deposited at the Gray Herbarium, the New York Botanical Garden, the United States National Herbarium, the California Academy of Sciences, Pomona College, Rancho Santa Ana Botanic Garden, San Diego Natural History Museum, Stanford University and the University of California, Berkeley.

Comparisons of Apogamous and Sexual Forms

Chromosome Numbers

Plants of the sexual type of *Pellaea andromedifolia,* from the San Gabriel mountains in southern California *(Alt 3)* and from Humboldt County in northern California *(Tryon & Tryon 5557)* have the normal complement of 16 spore mother cells and show at diakinesis that $n = 29$ with com-

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triploid, "n" = 87, Point Mugu, Calif., × 1300. d-e. *P. intermedia,* d. Mitotic cell from root tip, 2n = 58, Saltillo, Mexico, × 1300. e. Squash preparation of meiosis, apogamous triploid, "n" = 87, Chiricahua Mts., Arizona, × 2500. f-g. *P. ovata,* squash preparations of meiosis, f. Sexual diploid, n = 29, Gillespie Co., Texas, × 2000. g. Apogamous triploid, "n" = 87, San Luis Potosí, Mexico. × 650.

Fig. 2. Explanatory, enlarged diagrams for Fig. 1 showing chromosomes in focus in black and white and the remainder in outline. a-c. *Pellaea andromedifolia*, a. Sexual diploid, n = 29. b. Apogamous

plete and regular pairing (Figs 1a, 2a). Apogamous plants from Humboldt County in northern California *(Harris 21651)* resemble the sexual plants in leaf morphology, have sporangia with eight spore mother cells and at diakinesis show that "n" = 87 with complete and regular pairing of the chromosomes (Figs. 1b, 2b). Apogamous plants from Ventura County in southern California *(Kiefer 1132)* differ from apogamous plants from Humboldt County in having narrower leaves and pinnae of a more coriaceous texture. They have eight spore mother cells per sporangium and at diakinesis "n" = 87 with the chromosomes completely paired (Figs. 1c, 2c).

Plants of *Pellaea intermedia* grown from a collection from northern Mexico, east of Saltillo *(Rollins & Tryon 58144)* have 64 spores per sporangium. Mitotic cells from the root tips show chromosome figures of $2n = 58$ (Figs. 1d, 2d). Apogamous plants, morphologically similar to the sexual ones, grown from a collection from the Chiricahua mountains in southern Arizona *(Tryon & Tryon 5089)* show "n" = 87 at diakinesis and complete pairing (Figs. 1e, 2e). No 16-celled sporangia were observed.

Plants of *Pellaea ovata* of the sexual type which were grown from a specimen collected in Gillespie County in central Texas *(Tryon & Tryon 5029)* have the normal complement of 16 spore mother cells and the haploid chromosome number is — 29 (Figs. 1f, 2f). Apogamous plants grown from a collection from northern Mexico, near San Luis Potosí *(Rollins & Tryon 58222)* in leaf morphology closely resemble plants of the sexual type; only eight spore mother cells were observed and at diakinesis "n" = 87 chromosomes (Figs. 1g, 2g).

These cases of apogamy in triploid plants of *Pellaea* are similar to the classic example reported for *Pellaea atropurpurea* by Manton (1950) and also by Tryon and Britton

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triploid, "n" = 87. c. Apogamous triploid, "n" = 87. d-e. *P. intermedia,* d. Sexual diploid, 2n = 58. e. Apogamous triploid, "n" = 87. f-g. *P. ovata,* f. Sexual diploid, n = 29. g. Apogamous triploid, "n" = 87.

(1958) in *P. sagittata*. They are, however, unique in the occurrence of both sexual diploids and apogamous triploids which are of generally similar morphology, in each of the species. In *P. sagittata* the diploid var. *cordata* and the triploid var. *sagittata* are morphologically distinct — and in *P. atropurpurea* the triploid is the only known form. In these apogamous taxa, the problem which Manton alluded to as the "triploid dilemma" was explained in the case of *P. atropurpurea* as possibly arising as a back-cross between an allotetraploid and one of its diploid parents, largely on the basis of pairing relationships in the 16-celled sporangia.

In the three species reported here each sexual diploid form has most probably served as a parent in the cross producing a morphologically similar triploid. The second parent might be a tetraploid as suggested by Manton or possibly an autotetraploid originating from different races of the same species. Tetraploids are not known in these three species although they are known in the section and two of these are apogamous. Another possible parent is an apogamous diploid, as was reported in the formation of apogamous triploids in *Pteris* by Walker (1966). Plants of this constitution are not known in *Pellaea*. This record of both sexual diploid and apogamous triploid plants in three closely related species is of special interest for it appears that the parental forms in each of them share a capacity for generating the synchronized mechanism necessary for obligate apogamy.

Gametophyte and Juvenile Leaves

Illustration of the sexual and apogamous forms for comparisons of these stages in the life history is shown in *Pellaea andromedifolia* (Fig. 3). More detailed accounts of particular structures have been made by Atkinson, in Tryon and Britton (1958), Tryon (1960) and Nayar and Bajapi (1964).

Spores of both sexual and apogamous types germinate rapidly, usually between 6-15 days, and the prothallia also develop quickly with as many as 26 cells and a small plate in ten days. The mature structure is cordate and erect. In

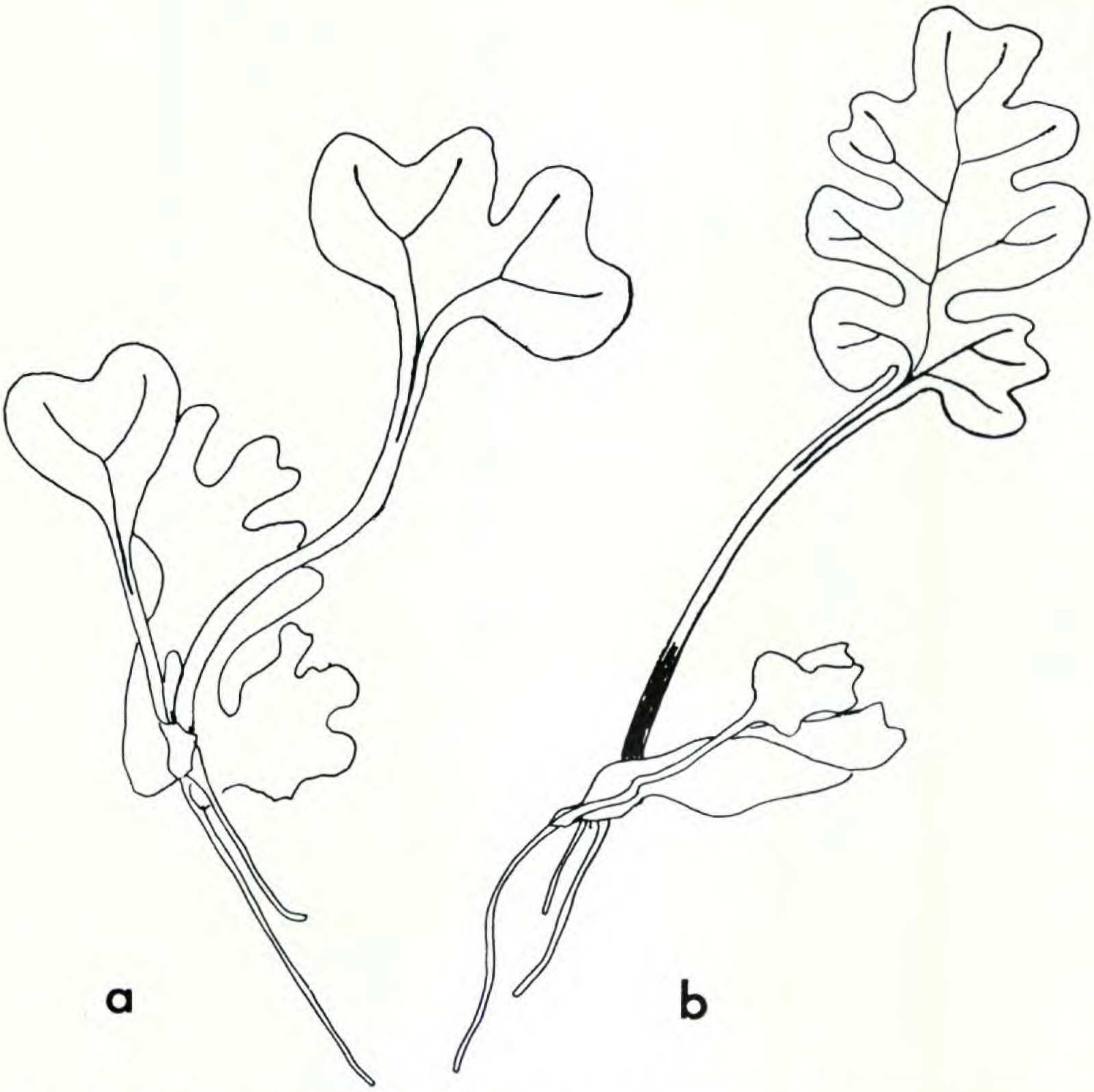

Fig. 3. Tracings of gametophytes and juvenile leaves of sporophytes, of *Pellaea andromedifolia,* at 6 months, × 5. a. Sexual diploid, gametophyte at base with several irregular lobes and the first two symmetrically lobed leaves of the sporophyte, from *Tryon & Tryon 5557.* b. Apogamous triploid, gametophyte and early leaf of sporophyte at base, the fifth leaf with deep, asymmetrical lobes, from *Tryon & Tryon 5556.*

the *sexual type* antheridia are produced first, usually after 15 days, and may be formed on plants with as few as 20 cells. They are confined largely to the lower surface in the posterior region, nearest the spore, and are abundant among the rhizoids. Archegonia are formed later than the antheridia, on a cushion of cells 2 or 3 layers thick, on the lower surface in the anterior region, a few cells behind the central notch. Among the rhizoids of large prothallia there may be several small prothallia bearing only antheridia. These seem to be of the form recognized by Stokey (1951) as ameristic and their development may promote outcrossing in these plants. Juvenile leaves on sexual plants have symmetrical lobes; the initial ones bilobed and later ones with more and deeper sinuses (Fig. 3a). The prothallus may persist after the formation of several leaves with continued production of antheridia on new lobes. The *apogamous type* germinates slightly earlier than the sexual one. One or both sex organs may be suppressed but usually antheridia are formed. Antherozoids are abundantly produced and appear normally developed. Archegonia are usually absent but non-functional ones were observed in *P. andromedifolia*, after young "embryos" were developed. "Embryos" develop, independent of sex organs, after two or three months, usually in the central portion of the prothallus, adjacent to the notch. They may be surrounded by slender, hyaline scales attached to the prothallus and young leaves. The first leaves of apogamous plants are often asymmetrical, and pinnate leaves resembling the mature form are produced earlier than on sexual plants (Fig. 3b). The different time of development and morphology of these structures in the apogamous forms appear to represent a repatterning of the similar growth systems in the sexual forms.

Precise ecological data are lacking for most collections of these species; however, in Humboldt County, California where both sexual and apogamous plants of *P. andromedifolia* grow together; the apogamous ones grow among rocks in exposed situations and the sexual often grow in humus in more shaded sites. The apogamous condition, eliminating the need for fertilization, would be advantageous to these species in occupying more xeric habitats. The evolutionary potential of the apogamous type is indicated by its adaptation to a different ecological niche.

Epidermis — Stomatal Guard Cell Size

The epidermal cells are of particular interest in these species since there is a correlation between the apogamous, polyploid condition and larger guard cell size. The epidermal

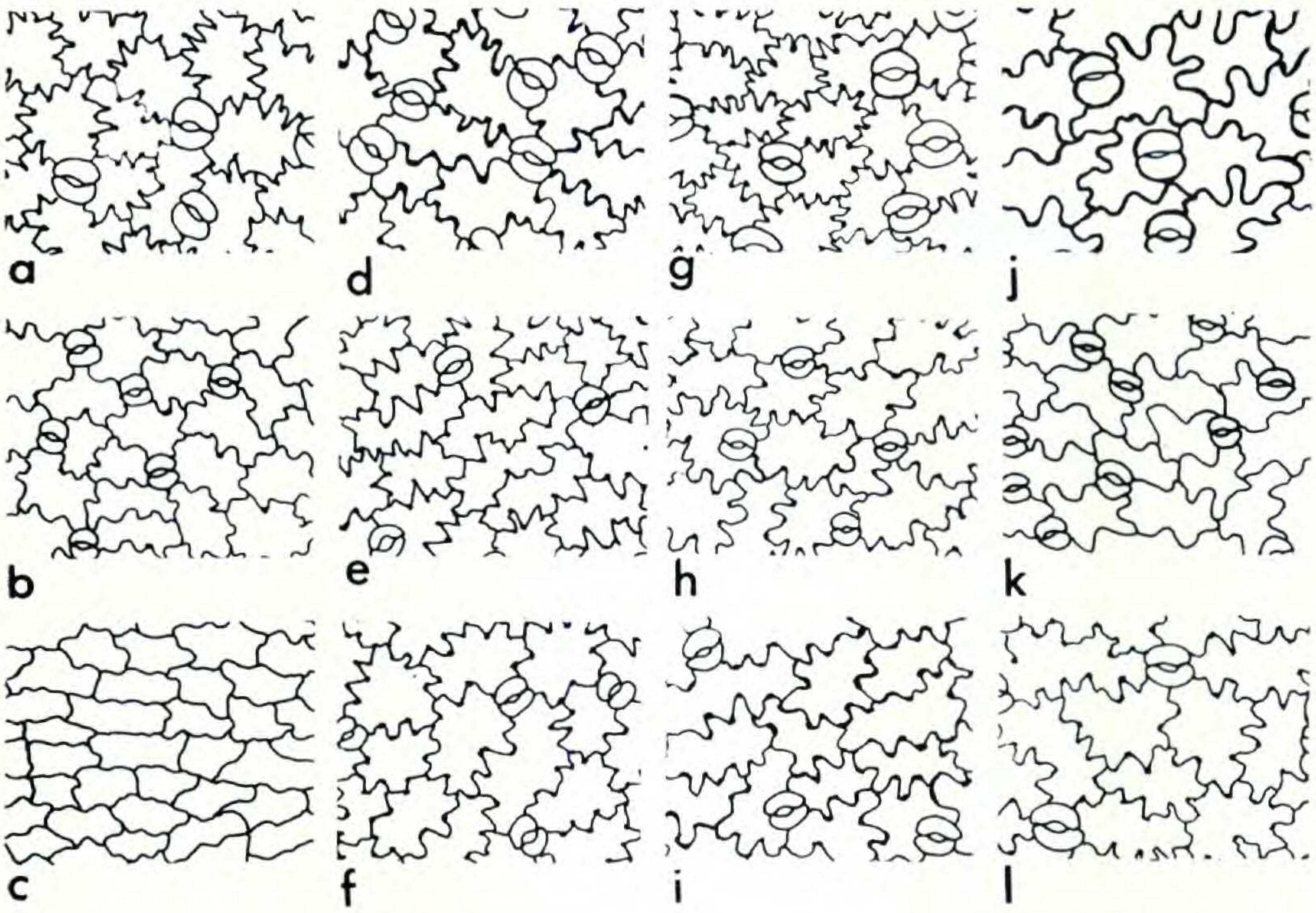

Fig. 4. Tracings of epidermal cell walls in *Pellaea*, × 80, of the abaxial surface with stomata, except c, adaxial surface. a-c. *Pellaea ovata*. a. 3×, *Correll 22792*. b. 2×, *Tryon & Tryon 5029*. c. 3×, *Rollins & Tryon 58222*. d-f. *P. andromedifolia*. d. 3×, *Harris 21651*. e. 2×, *Alt 3*. f. 2×, *Tryon & Tryon 5557*. g-h. *P. intermedia*. g. 3×, *Tryon & Tryon 5089*. h. 2×, *Rollins & Tryon 58144*. i. *P. myrtillifolia*, *Wagenknecht 946*, Chile. j-k. *P. ternifolia*. j. 4×, *Tryon & Tryon 5141*. k. 2×, *Tryon & Tryon 5105*. l. *P. rufa*, *Schelpe 4939*, South Africa.

cells of the abaxial surface, are photosynthetic and the guard cells which are confined to this surface, may develop against either one or two walls of the stomatal initial and are densely packed with chloroplasts. In the three species in *Pellaea* examined the abaxial epidermal cells have peculiar anticlinal walls that are sharp-angled with irregularly thickened peaks and sinuses. This is one of the features, along with the slender, creeping rhizome with bicolorous scales and small, ovate segments, characterizing these three species and two others allied to *P. andromedifolia*. Tracings of the walls from a microprojector are illustrated (Fig. 4) for all five species in this group and also for *P. ternifolia* representing

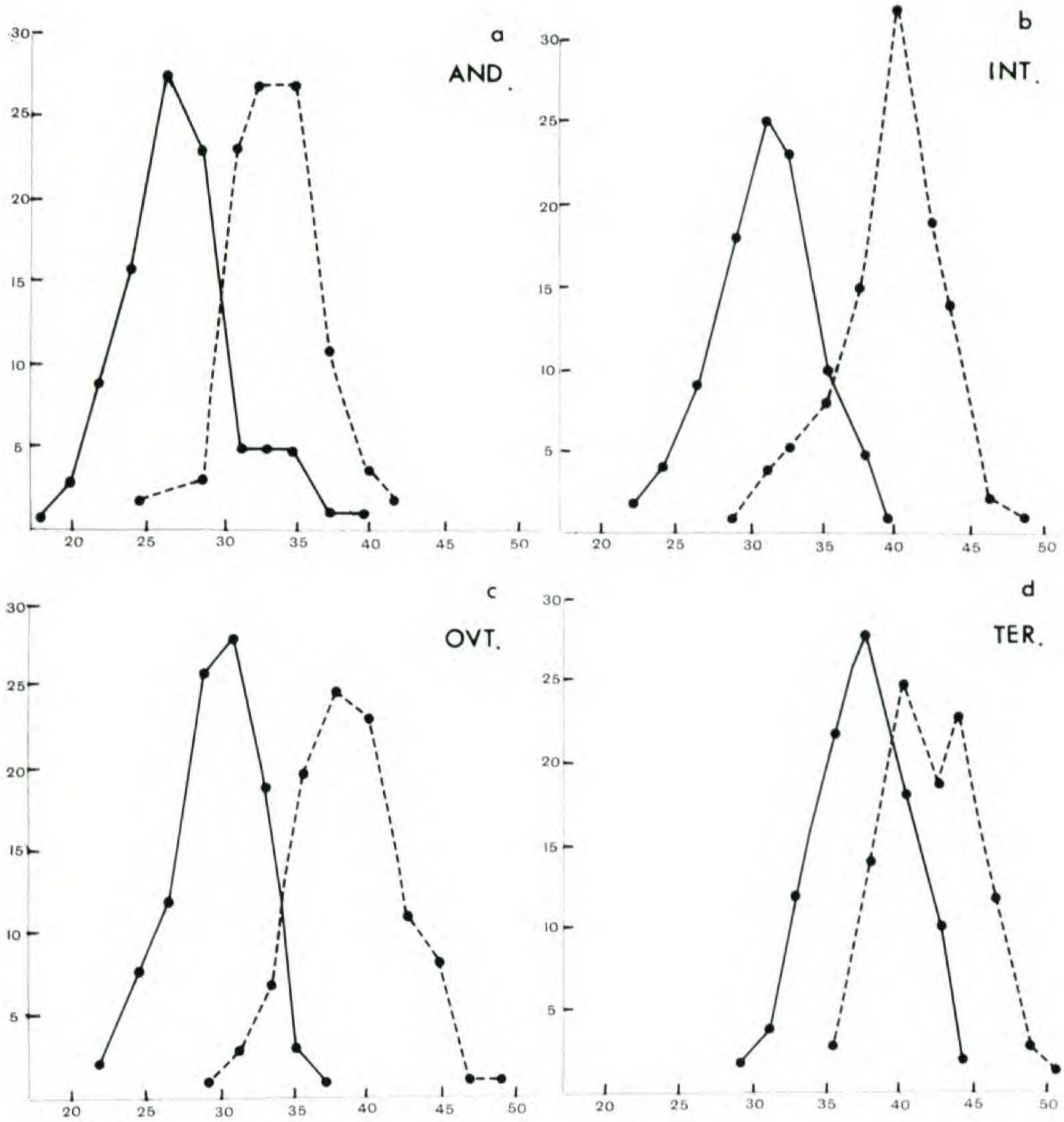

Fig. 5 a-d. Length of longer guard cell in 100 stomata; abscissa-guard cell length in micra; ordinate-frequency and %. a. *Pellaea andromedifolia*, solid line, sexual diploid, *Tryon & Tryon 5557;* broken line, apogamous triploid, *Tryon & Tryon 5556*. b. *P. intermedia*, solid line, *Rollins & Tryon 58144;* broken line, apogamous triploid, *Tryon & Tryon 5089*. c. *P. ovata*, solid line, sexual diploid, *Tryon & Tryon 5029;* apogamous triploid, *Rollins & Tryon 58222*. d. *P. ternifolia*, solid line sexual diploid, *Tryon & Tryon 5105;* broken line, sexual tetraploid, *Tryon & Tryon 5141*.

another group in the genus. The greater size of the guard cells in the apogamous and polyploid plants in the top row, compared to those in the center row, can be readily seen. The pattern of epidermal cells on the adaxial surface is also illustrated for *P. ovata* (Fig. 4c). These have a different form with shallowly undulate walls, which are uniform in thickness and the cells are mostly longer than broad. In Fig. 5 a-c measurements showing the guard cell length are based on the larger member in each of 100 stomata, for both sexual and apogamous plants, plotted to the first decimal. In each species these illustrate the smaller guard cell size in the sexual diploid race as compared to the apogamous triploid. In the text the ranges are given by summation to the nearest whole number. In *P. andromedifolia* the range in length of the guard cells (Fig. 5a) in a sexual diploid plant from northern California is 18-40μ, with a mean of 27. The range of an apogamous triploid plant from the same area is 24-42μ with a mean of 34, which is 26% larger than the sexual. In *P. intermedia* the range in guard cell length (Fig. 5b) of a sexual diploid plant from northeastern Mexico is 22-40μ with a mean of 31. An apogamous triploid plant from southern Arizona has a range of 28-48μ with a mean of 39, which is about 26% greater than the sexual type. In *P. ovata* the range in guard cell length (Fig. 5c) of a sexual diploid plant from central Texas is 22-37μ with a mean of 30. An apogamous triploid plant from north-central Mexico ranges from 29-48μ with a mean of 38, which is about 27% larger than the diploid.

The data from these apogamous and polyploid races may be compared with that from *P. ternifolia,* in which a sexual polyploid race is known. In Fig. 5d the measurements of the guard cells are given for a sexual diploid and for a sexual tetraploid of *P. ternifolia.* The sexual diploid plant from southcentral Mexico ranges from 29-44μ with a mean of 37. The sexual tetraploid from the same region ranges from 35-51μ with a mean of 42, which is 14% larger than the diploid. The increase in size of guard cells in the polyploid over the diploid in the sexual *P. ternifolia,* with a 1:2 ratio in chromosome number of diploid to tetraploid, is significantly less than the 26% or 27% increase in the apogamous polyploids over the other three species having a 2:3 ratio of chromosome number in the diploid to triploid levels. This suggests that apogamy may be a factor in the increase in the size, augmenting, in these examples, the well known effect of polyploidy.

The epidermal patterns for two species of the group in which apogamy is not reported are also included (Figs. 4 i, 1). The average guard cell size of *P. myrtillifolia*, an endemic in north Chile, is 39μ and that in *P. rufa*, which occurs in the South African Karroo, is 38μ. The chromosome numbers are not reported but both species have the normal complement of 64 spores. The average size of the guard cells in these corresponds to that of the polyploid forms in the previous sets and suggests that they may be polyploid.

Spores

The apogamous condition in ferns is most readily detected by 32 spores per sporangium which is half the normal complement in most leptosporangiate species. In apogamous plants having well developed spores this number is consistent at either diploid, triploid or tetraploid levels. The mechanism accounting for this departure from the normal is the premeiotic doubling of chromosomes along with arrested cytoplasmic cleavage, prior to the formation of spore mother cells. These changes result in eight rather than the normal number of 16 spore mother cells.

The spores of both the sexual and apogamous forms in *P. andromedifolia*, *P. intermedia* and *P. ovata* are generally morphologically similar. They are tetrahedral-globose, trilete and, in amb, biconvex. They are pale yellow with excrescences in the outer layer of the spore wall forming rugae which fuse into irregular reticula. The rugae are irregular, flattened and wing-like in surface view and appear as moderately sharp projections in profile. Three commissural ridges protrude slightly from the surface and extend to the equatorial region. However, spores of apogamous plants differ from those of sexual plants in having more numerous and more prominent rugae as well as a larger size and a smaller number per sporangium. Spores of apogamous plants may also show marked variation in the form of the commissural ridges. They may be trilete, as in spores of sexual plants, or they may have only a single ridge or a dense rugose patch asymmetrically placed on the proximal face. The monolete spores which frequently occur in apogamous plants appear to become dissociated from the tetrad early in their development.

Measurements of the greatest diameter of 100 spores from plants of each of the races of these three species are presented in graphs (Fig. 6 a - c). In these, size has been plotted to the first decimal. In the text the decimal has been elminated by summation to the nearest whole number. In *P. andromedifolia* the range in spore size (Fig. 6a) of

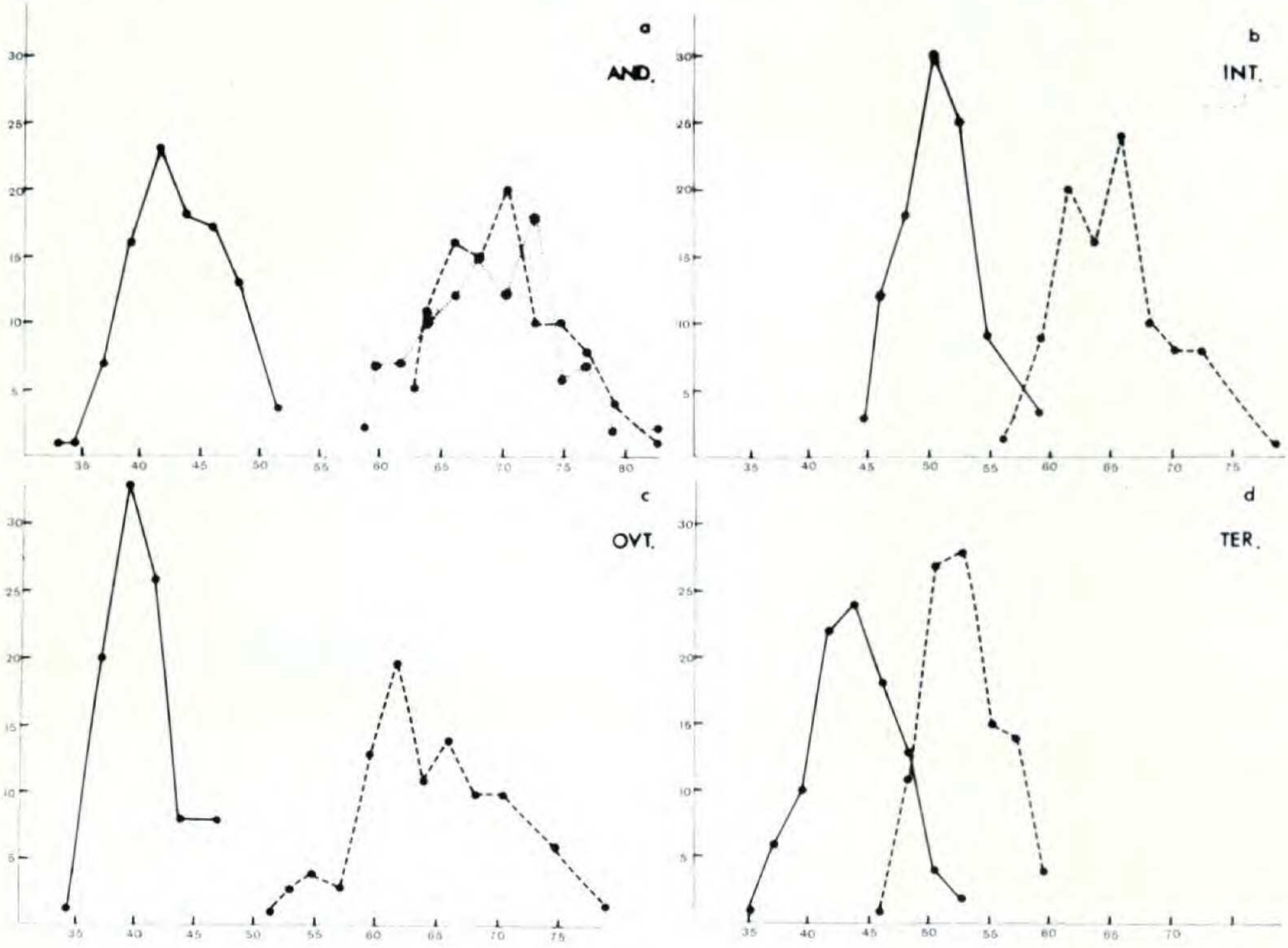

Fig. 6 a-d. Length of longest diameter in 100 spores; abscissa-length in micra; ordinate-frequency and %. a. *Pellaea andromedifolia,* solid line, sexual diploid, *Alt 3;* dashed line, apogamous triploid, *Harris 21651;* dotted line, apogamous triploid, *Kiefer 1132.* b. *P. intermedia,* solid line, sexual diploid, *Rollins & Tryon 58144;* broken line, apogamous triploid, *Rollins & Tryon 58306.* c. *P. ovata,* solid line, sexual diploid, *Tryon & Tryon 5029;* broken line, apogamous triploid, *Rollins & Tryon 58222.* d. *P. ternifolia,* solid line sexual diploid, *Rollins & Tryon 58218;* broken line, sexual tetraploid, *Tryon & Tryon 5141.*

a sexual plant from southern California is is 34 - 52μ, with a mean of 44. Spores from an apogamous plant from the southern portion of the state range from 59 - 83μ, with a mean of 70 which is 59% larger than the sexual. Spores from an apogamous plant from the northern part of California range from 63 - 83μ and have a mean of 71 which is 61% larger than the spores of the sexual plant. In *P. intermedia* (Fig. 6b) spores of the sexual plant range from 44 - 59μ with a mean of 52, while those of the apogamous plant range from 56 - 79μ with a mean of 66, which is about 27% larger than those of the sexual plant. In *P. ovata* (Fig. 6c) spores of the sexual plant range from 34 - 47μ with a mean of 41 and those of the apogamous plant range from 52 - 79μ, with a mean of 66 (61% larger than the sexual plant). In the graphs illustrating these ranges in spore size, it may be seen that there is no or little overlap in sizes of the sexual and apogamous members in each of the three species. These appear in contrast to the graph showing spore sizes in *P. ternifolia* (Fig. 6d). Here spores from a sexual diploid plant range from 35 - 53μ with a mean of 44, while those of the sexual tetraploid range from 46 - 59μ, average 54 (23% larger), with a clear overlap. The influence of apogamy on the size of the spores is not evident. The ratios of cell size, based on chromosome level, in the diploid to triploid is 1 : 3 and of the diploid to tetraploid is 1 : 2. Thus the effect of apogamy on spore size is obscured by differences in the chromosome levels. The extent of variation in spore size of apogamous plants is clearly greater than that shown by the sexual plants. This contrasts with the condition in the sexual diploid and tetraploid and suggests that the process of spore formation is not as strongly controlled in the apogamous plants.

The larger spore size in the tetraploid *P. ternifolia* may be useful in distinguishing different cytotypes in the herbarium specimens. In the apogamous plants differences in spore number and size have utility in determining the ranges of cytotypes from herbarium material and such ranges may supply useful information on the geographic centers and migration of the species.

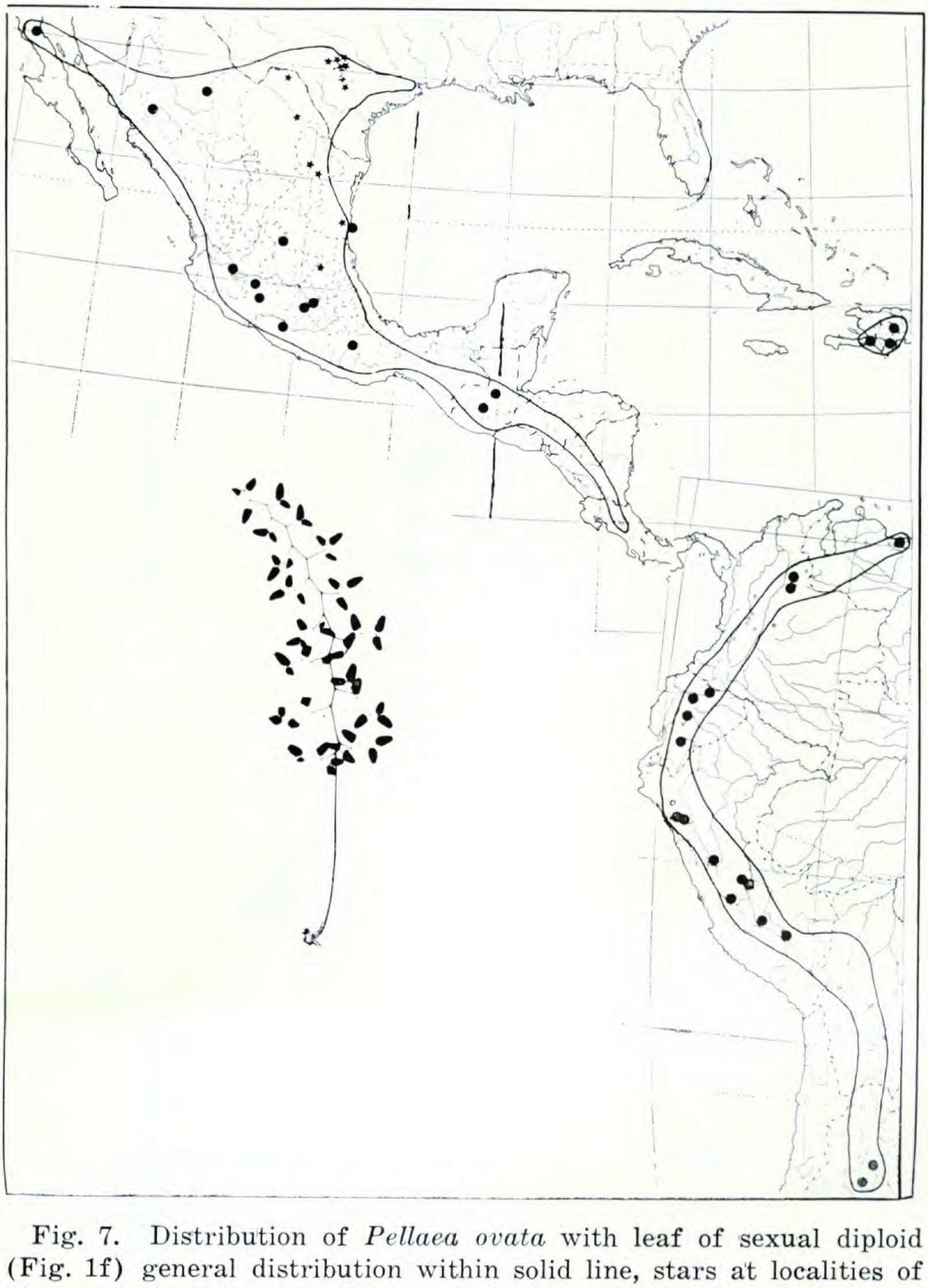

Fig. 7. Distribution of *Pellaea ovata* with leaf of sexual diploid (Fig. 1f) general distribution within solid line, stars at localities of 64-spored, sexual plants; dots at localities of 32-spored, apogamous plants.

Geographic Distribution

The general distribution of the species is shown in Figs. 7-9 by solid lines; the dots representing localities of

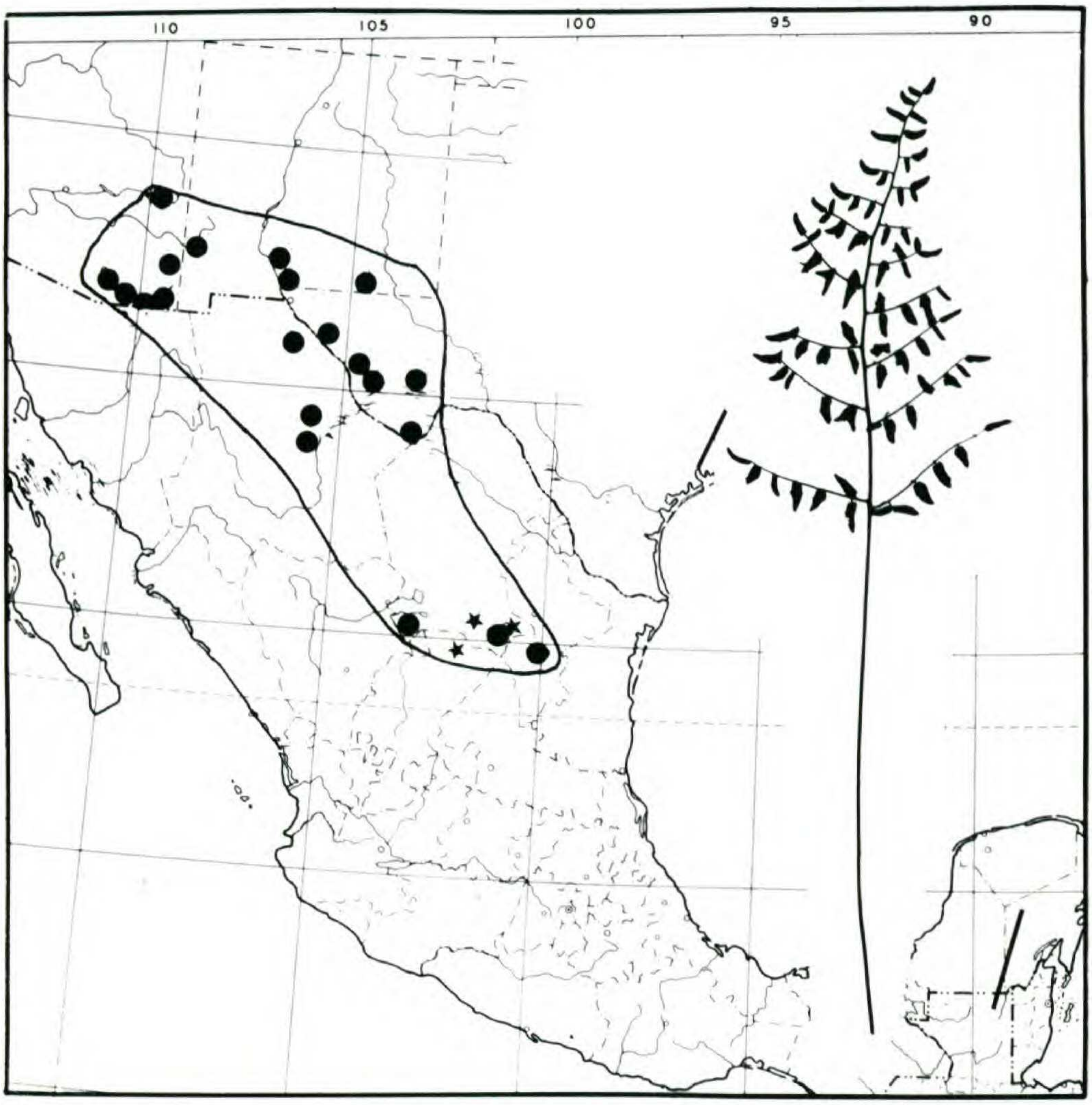

Fig. 8. Distribution of *Pellaea intermedia* with leaf of sexual diploid (Fig. 1d) general distribution within solid line, stars at localities of 64-spored, sexual plants; dots at localities of 32-spored, apogamous plants.

apogamous plants and stars the sexual ones, based on spore counts of material with sporangia intact. The silhouettes show the general shape of the leaves for each species and are taken from cytologically determined diploid plants. It is expected that additional material and field study will extend the ranges. However, these data are adequate to represent the general patterns. In these species, as in others where such distributions have been plotted, the apogamous races are generally more wide ranging. In *P. ovata* (Fig. 7), which has one of the most extensive ranges in the

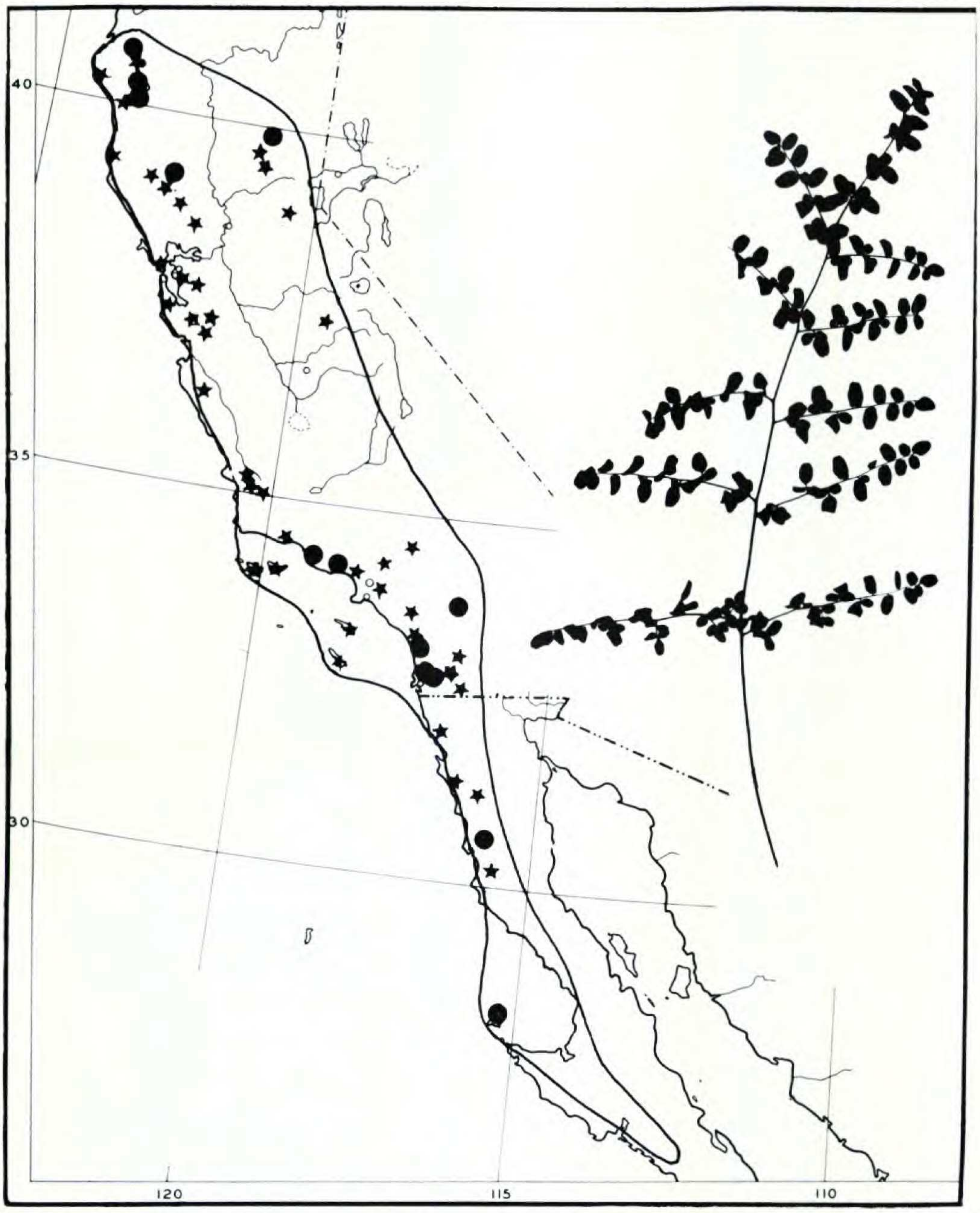

Fig. 9. Distribution of *Pellaea andromedifolia* with leaf of sexual diploid (Fig. 1a) general range within solid line, stars at localities of 64-spored, sexual plants; dots at localities of 32-spored apogamous plants.

genus, plants having the normal 64-spored sporangia are limited to central Texas and adjacent northeastern Mexico. All specimens from South and Central America, the Caribbean area and southern Mexico have 32 spores and are of the apogamous form. The range of *P. intermedia* (Fig. 8) is restricted to the southwestern United States and adjacent northeastern Mexico. Plants with 32-spored sporangia are widely distributed in Texas, New Mexico, Arizona and northern Mexico while plants with 64 spores are known only from the region around Saltillo, Mexico. The distribution of sexual and apogamous plants in *P. andromedifolia* (Fig. 9) contrasts with the ranges of the previous species. Plants with 32 spores are disjunct, occurring in northern California in Humboldt County, and in southern California near Palm Springs and along the coast near San Diego south into Baja California and in adjacent Cedros Island. Both sexual and apogamous races occur within the same region and in Humboldt County they grow a few meters apart.

The ranges of the apogamous races of these three species may be compared with other apogamous pellaeas to provide a broader basis for an evaluation of the phenomenon. One measure of the evolutionary success of apogamous species is the extent of their geographic range. This is particularly applicable in comparison with the ranges of closely related sexual species. Apogamy is reported in six of the 15 species in section Pellaea and in four, the apogamous races have wide ranges in North America or in both North and South America. In two species the apogamous types have been distinguished as varieties and are far wider ranging than the sexual counterpart. Thus, on the basis of their more extensive distributions, four of the apogamous forms are more successful than related sexual ones. The distribution of *P. intermedia* is not extensive, but within it the apogamous race has a broader distribution than the sexual race. There are some collections of *P. intermedia* from the Chisos mountains in Texas, within the range of the apogamous type, bearing on a single leaf some sporangia with 32 well-developed spores and others with a larger number of undeveloped spores. In *P. andromedifolia* the apogamous race is disjunct and not as abundant as the sexual one. This contrasts with the distributions shown in the other species in which the apogamous race predominates, and suggests the possibility of a different evolutionary history in *P. andromedifolia.*

SUMMARY

Comparisons were made of epidermal cell and spore size of sexual diploid and apogamous triploid forms in three closely related species of *Pellaea* in a study of the effect of apogamy on morphological characters. Comparisons were also made with sexual diploid and sexual tetraploid forms in another species and with other members of *Pellaea.* Size of stomatal guard cells of the apogamous triploid plants relative to the sexual diploids in each of the species, was greater than would be expected on the basis of the chromosome levels alone. The same effect was not evident in comparisons of spores. In these cells the large size of the apogamous triploids relative to the sexual diploids was of the order that would be expected from the different chromosome levels.

Comparisons of the geographic distribution patterns of the sexual and apogamous races and with those of other members of the genus show that the apogamous types are wider ranging. However, in *P. andromedifolia* apogamous plants have a disjunct distribution and are not as abundant as the sexual ones.

The evolutionary potential of apogamous plants is shown in their production of functional antherozoids, their adaptation to different ecological niches, and their broad distributions. In these pellaeas differences in the ranges of the apogamous and sexual types are interpreted here as reflecting the dynamics of these reproductive systems in natural populations.

CHROMOSOME NUMBERS OF PELLAEA

Species	Locality and Collection	Mode of repro-duction	Meiotic chromosome numbers	Ploidy
P. andromedifolia (Kaulf.) Fée	San Gabriel Mts. California *Karen Alt 3* — Fig. 1a	Sexual	29	2X
	Humboldt Co. California *S. Harris 21651* — Fig. 1b	Apogamous	87	3X
	Humboldt Co. *R. M. & A. F. Tryon 5557*	Sexual	29	2X
	Humboldt Co. *R. M. & A. F. Tryon 5556*	Apogamous	87	3X
	Point Mugu, Ventura Co., California *L. Kiefer 1132* — Fig. 1c	Apogamous	87	3X
P. intermedia Mett. ex Kuhn	Saltillo, Mexico *R. C. Rollins & R. M. Tryon 58144* — Fig. 1d	Sexual	29 (from 2n = 58)	2X
	Chiricahua Mts. Arizona *R. M. & A. F. Tryon 5089* — Fig. 1e	Apogamous	87	3X
P. ovata (Desv.) Weatherby	Gillespie Co., Texas *R. M. & A. F. Tryon 5029* — Fig. 1f	Sexual	29	2X
	San Luis Potosí, Mexico *R. C. Rollins & R. M. Tryon 58222* — Fig. 1g	Apogamous	87	3X
P. ternifolia (Cav.) Link var. *ternifolia*	Cuernavaca, Mexico *R. M. & A. F. Tryon 5105*	Sexual	29	2X
	San Luis Potosí, Mexico *R. C. Rollins & R. M. Tryon 58218*	Sexual	58	4X

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